The milliped family Trichopetalidae, Part 1: Introduction and Genera *Trigenotyla* Causey, *Nannopetalum* n. gen., and *Causeyella* n. gen. (Diplopoda: Chordeumatida, Cleidogonoidea)

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Abstract

Introductory materials for a revision of the milliped family Trichopetalidae are presented, and the species of three of the five genera are described (*Nannopetalum* n. gen.*, Trigenotyla* Causey, 1951, *Causeyella*, n. gen.*).* *Nannopetalum* is related to *Trichopetalum*, and includes three new species from the Appalachian piedmont: *N. pattersonorum* (Virginia)*, N. vespertilio* (North Carolina)*,* and *N. fontis* (Alabama)*. Trigenotyla* Causey includes four species: *T. parca* Causey (Arkansas), *T. vaga* Causey (Oklahoma), *T. blacki* n. sp. (Oklahoma), and *T. seminole* n. sp. (Oklahoma). *Causeyella* n. gen. is based on *Scoterpes dendropus* Loomis (Missouri and Arkansas), and also contains two new species: *C. causeyae* n. sp. (Arkansas) and *C. youngsteatorum* n. sp. (Arkansas). *Causeyella* and *Trigenotyla* are closely related.

Key Words: Milliped, Diplopoda, Chordeumatida, Cleidogonoidea, Trichopetalidae, *Trigenotyla, Causeyella, Nannopetalum, Trichopetalum, Scoterpes, Zygonopus, Mexiterpes,* taxonomy, North America, troglobionts

Introduction

The millipeds of the chordeumatidan family Trichopetalidae Verhoeff, 1914, range in size from small to minute (close to the apparent size minimum for chilognath millipeds), are found in soil and litter or as obligate cave inhabitants, and are for the most part winter-active. Given these characteristics, it is not surprising that a revision of the family has never been attempted, that accurate illustrations of many of the described species have never been published, and that a substantial portion of the species in the family have not been named or described. Of the major chordeumatidan families of North America, only the Trichopetalidae have never been given a first revision. Despite the lack of fundamental knowledge of the diversity, classification and phylogeny of the trichopetalids, these

small millipeds hold great promise as tools for the study of speciation and biogeography. Some trichopetalids are quite widespread, single epigean species being found over broad areas of the eastern United States and adjacent Canada. Other, troglobitic species seem restricted to individual cave systems or karst areas, and still others, though troglobitic, have surprisingly extensive distributions within which little variation in morphological characters can be detected. Yet there are indications from early electrophoretic studies (Laing, Carmody and Peck, 1975) that within this latter group, molecular methods may not only reveal sibling or cryptic species, but provide clues to the timing and mechanisms by which these species have formed. Such work would be facilitated by the fact that many troglobitic trichopetalids usually maintain large, thriving populations that can be repeatedly sampled, and are rather easily and reliably collected at almost any time of year from the caves in which they are found.

The focus of the present study, however, is on the taxonomy of this neglected family, and I will attempt to lay down a systematic framework within which future knowledge can be placed. The present part of the planned two-part project introduces the family and deals with three smaller genera, two of them new. The second part will cover the two large genera, *Scoterpes* and *Trichopetalum,* and provide a phylogenetic analysis.

Trichopetalids belong to the milliped order Chordeumatida, probably the second-most diverse order (after Polydesmida) of the Class Diplopoda. Chordeumatidans are most speciose in the North Temperate Zone, particularly in Europe and North America, though they also can be found in Australia and New Zealand, Madagascar, Sri Lanka, tropical southeast Asia, and temperate South America west of the Andes. Our knowledge of the millipeds of temperate Asia remains woefully sketchy, but there is every reason to think that chordeumatidans are highly diverse in China (i. e., Shear, 2000, 2002).

Chordeumatidans are minute to medium-sized millipeds (3–35 mm long) that may easily be recognized by the six characteristic macrosetae found on each trunk diplosegment, coupled with an absence of the repugnatorial pores found in most other millipeds. Close examination reveals a pair of spinnerets on the telson. Among chordeumatidans, trichopetalids are a part of the superfamily Cleidogonoidea, a taxon now recognized as containing the most primitive chordeumatidans (Shear, 2000).

Cleidogonoids are found in Eastern North America and Mexico, the Iberian Peninsula, the Balkans, and in the Himalaya. Their plesiomorphic position within the Chordeumatida is established by the form of the ninth legpair of the males, often strongly reduced in size and segmentation (as in the trichopetalids) but more typically still quite leglike. In apomorphic chordeumatidans, this leg becomes modified as an accessory gonopod and can even take over the spermatophore-transfer function from the primary gonopods, formed from the eighth legpair. In such species it may lose all resemblance to a walking leg. However, among cleidogonoids this function rarely or never develops, and the ninth legpair appears reduced simply to get it out of the way of the functional gonopods formed from the eighth legs. In some families, lobes on the ninth leg coxae may serve to lock the

gonopods in a retracted position until mating occurs. Additionally (as in trichopetalids) the ninth legpair may carry a vestigial pair of coxal glands. Besides Trichopetalidae, the superfamily includes the families Cleidogonidae, Entomobielziidae, Lusitaniosomatidae (both probably synonyms of Cleidogonidae) and Opisthocheiridae.

Trichopetalids are easily distinguished from these other families by a number of characters, the most obvious of which is the extraordinary development of the segmental setae, which are so long and stout in species of *Scoterpes* Cope, 1872, that they create a superficial resemblance in these millipeds to dermestid beetle larvae. In *Scoterpes* species the setae equal or exceed in length the width of the body. No other chordeumatidans have such large setae, though conotylids of the genus *Bollmanella* Chamberlin, 1941, found outside the range of the trichopetalids in California, Oregon and Washington, approach this condition. A sticky secretion is evidently produced at the base of each seta which is frequently seen in preserved specimens as a coagulated blob about halfway up the length of the seta. In most species, the segmental setae are longitudinally grooved, perhaps to facilitate the movement of this secretion to the setal tips (Fig. 32).

Further, the ninth legs of male trichopetalids are usually reduced to just two podomeres, sometimes with one or a few vestigial distal podomeres. The second apparent podomere is reflexed laterodorsally, and evidently results from the fusion of all the telopodite podomeres (but see the discussion of *Trigenotyla* below), since a rudimentary claw is often present at the tip, and vague divisions between distal podomeres, along with remnants of musculature, can be discerned (Figs. 4, 7, 18, 24, 26, 31). No coxites are found on these limbs, and they are only slightly adapted to support the gonopods. Evidently they are reduced in size and shape simply to allow access by the gonopods to the spermatophore-forming glands of the tenth and eleventh leg coxae. Further evidence of plesiomorphy is the presence, in at least some individuals of several species, of vestigial coxal glands on the ninth legs (Figs. 14, 24, 26), serial homologs of the functional ones on the tenth and eleventh legpairs; in many other chordeumatidan families the permanently extruded, sclerotized glands of the ninth legpair form elaborate colpocoxites.

Not much is known of the natural history of these obscure little animals. Species of *Trichopetalum* Harger, 1872, seem almost always to be found in association with wet or continually damp litter, usually from deciduous trees. Sensitive to heat and drying, *Trichopetalum* specimens become immobile and moribund within a minute or two if held in the hand. Because of their small size, they are often overlooked by collectors and are most easily taken by Berlese or Tullgren sampling. Species of *Scoterpes, Causeyella* n. gen., *Mexiterpes,* the subgenus *Zygonopus* Ryder, 1881, and some species of *Nannopetalum* n. gen., appear to be limited entirely to subterranean habitats, for which they are highly adapted, being depigmented and often eyeless, with elongated legs and antennae. Some *Scoterpes* can be maintained for at least a while if kept cool and at 100% humidity in a container floored with soil from their native cave. The food of no trichopetalid is known, but probably consists of well-decayed organic debris; cave species are most often seen on

logs, boards, leaves or guano. Gut contents of *Scoterpes* species are usually amorphous, with no identifiable material present even under high magnification, so one guess as to their feeding habits would be that they scrape bacteria from the surfaces of decaying wood. There are few recorded observations on mating, egg-laying, development, or life history. Barr (1967), in a study of *Scoterpes copei* (Packard) at Mammoth Cave National Park, Kentucky, found that individuals of this species live up to nine years. They may reproduce at almost any time of the year when maturity and resources permit. *Scoterpes copei* were characterized by Barr as mobile, searching over relatively wide areas of their habitat for thinly distributed food sources.

Trichopetalids are found only in eastern North America and the mountainous regions of northeastern and central Mexico. *Trichopetalum* occurs from Newfoundland, southern Ontario, and the northeastern United States west to Michigan and Wisconsin, thence southward to the northernmost parts of Mississippi, Alabama and Georgia in the east and to northern Arkansas and eastern Oklahoma in the west; species of *Trichopetalum* in the subgenus *Zygonopus* are limited to caves along the border between Virginia and West Virginia. *Trichopetalum* seems to be absent from the coastal plain from Virginia to South Carolina.

The related new genus *Nannopetalum* includes three species known from a few localities in the Appalachian Piedmont from Virginia to Alabama.

Eyeless, depigmented *Scoterpes* species are entirely cave-limited, and can be found from southern Indiana south through Kentucky and Tennessee to northern Alabama and Georgia. *Scoterpes* is absent from the karst regions of the Shenandoah Valley, West Virginia, and southwestern Virginia.

Trigenotyla has four species, each known from a few localities in Arkansas and Oklahoma. Two of these species, *T. blacki* and *T. seminole* (both new) are possibly troglobitic.

The new genus *Causeyella* consists of three species of obligate troglobites of Missouri and Arkansas, related to *Trigenotyla*. Its type species, *C. dendropus* (Loomis) was originally described in *Scoterpes*.

The seven species of *Mexiterpes* are found only in caves in the Mexican states of Guerrero, Queretaro, San Luis Potosi, and Tamaulipas. Most species are depigmented and have reduced eyes, and are known at present from single caves or cave systems.

Historical Overview of Trichopetalid Studies

The first trichopetalid milliped to be discovered was a troglobitic species, described by A. S. Packard in 1871 as *Spirostrephon copei*. It came from Mammoth Cave, in Kentucky. The following year, Cope (1872) placed this species in his new genus *Scoterpes,* and Harger (1872) named another new genus, *Trichopetalum,* for his own new species *T. lunatum,* collected in New Haven, CT (Harger's *Trichopetalum iuloides* is a caseyid of the genus *Underwoodia* Cook & Collins, 1895). A third new genus and species, *Zygonopus whitei,* was added in 1881 by Ryder; the specimens were found in Luray Caverns, Virginia.

Some confusion began to be introduced already in 1893 by the erratic young C. H. Bollman, who synonymized *Zygonopus* and *Trichopetalum* with *Scoterpes,* and included a species (*bollmani* McNeill) which we now know to be member of the conotylid genus *Conotyla* Cook & Collins, 1895 (Bollman's own *Scoterpes wyandotte,* described in 1888, is a synonym of *C. bollmani*).

All these early descriptions contained significant errors of observation or interpretation, probably due in part to the inadequate optical equipment of the day, and to the unfamiliarity of the authors with diplopods. At the time they wrote, all chordeumatidan millipeds were included in a single family, Craspedosomatidae Gray 1843. In 1895, O. F. Cook and G. W. Collins published the first really comprehensive, modern paper on North American millipeds, "The Craspedosomatidae of North America", and offered corrections to the earlier descriptions, as well as describing two additional species of *Trichopetalum, T. album* and *T. uncum.* They implied that *Scoterpes, Zygonopus* and *Trichopetalum,* all of which they recognized as distinct, were closely related to *Conotyla,* one of their new genera. Cook and Collins (1895) also included Packard's (1883) enigmatic *Polydesmus ocellatus* as *Trichopetalum(?) ocellatum,* but this species, described from Oregon, must not be a trichopetalid; Hoffman (1999) suggested a rhiscosomidid identity, which certainly fits the description.

Almost immediately afterwards, Cook (1896) divided up the North American Craspedosomatidae into several new families, including Conotylidae, into which he placed the three known trichopetalid genera. While understandable, this placement was incorrect. It was not set right until 75 years had passed (Shear 1971).

A careful study of the male genitalia convinced Verhoeff (1914, 1932) that *Trichopetalum* was the type of a new family, Trichopetalidae. However, the family continued to be regarded as a close relative of the Conotylidae Cook, 1895, and for some years the prolific North American specialist Nell B. Causey treated Trichopetalinae as a subfamily of Conotylidae (i.e., Causey, 1951). Evidently the reason for this was the superficial resemblance of the male ninth legs (then called posterior gonopods) in the two families: both have two apparent podomeres, with the apical one turned dorsally. However, the apical, or reflexed, podomeres are not homologous, being composed in the Conotylidae of only the femur, enlarged and swollen, and in the Trichopetalidae of all the telopod segments fused. The basal, or descending, podomere is the prefemur in conotylids and the coxa in trichopetalids (Shear 2000; this study). Conotylid ninth legs also invariably bear coxites which participate to some degree in spermatophore transfer, while this is never the case in trichopetalids.

No revisionary work on trichopetalids followed Verhoeff's proposal of the family name, but new genera and species were added through the next four decades. Most importantly, Chamberlin (1940) named a new genus for his *Tynopus dux,* from North Carolina, and Causey (1951) set up two new genera, *Flagellopetalum* and *Trigenotyla.* The latter generic name uses a combining stem from the Conotylidae, and signifies Causey's views

on the relationships of trichopetalids. *Flagellopetalum stannardi* Causey was from Illinois; *Trigenotyla parca* Causey from Arkansas.

In 1939 and 1943, H. F. Loomis added new species of *Scoterpes,* including *S. dendropus* (Loomis, 1939), from Missouri. His species is made the type of a new genus, *Causeyella,* in this study. Palmén (1952) found *Trichopetalum lunatum* at four localities in southwestern Newfoundland, and provided some excellent illustrations. In 1960, R. L. Hoffman weighed in with an important paper on the gonopod anatomy of the conotylids, in which he affirmed the distinct position of the trichopetalids, a conclusion later accepted by Causey (1969). The latter author had meantime been studying Mexican cave millipeds, and had named two new genera, *Mexiterpes* (Causey, 1963) and *Poterpes* (Causey, 1969), to include troglobitic trichopetalids from Mexico. Earlier, in 1960, Causey had published the first revisionary study of a trichopetalid genus, in which she added three new species to *Zygonopus.*

My first look at trichopetalids came in 1971 (Shear, 1971) in the context of a re-examination of all North American Chordeumatida. I concluded that the relationships of the trichopetalids were really with the Cleidogonidae (designating a superfamily Cleidogonoidea to include them both), based on similar gonopod plans, which differ significantly from those found in the Conotylidae and other heterochordeumatideans (see also Shear, 2000), the presence of a promentum in the gnathochilarium, coxal glands on legpair 11, and the form of the ninth legpair. I further concluded that *Zygonopus, Tynopus* and *Flagellopetalum* could not be maintained separate from *Trichopetalum,* and that *Poterpes* was a synonym of *Mexiterpes.*

That same year, Loomis and Schmitt (1971) surprisingly named two new genera and species of trichopetalids from Montana: *Endopus parvipes* and *Orthogmus oculatus.* Both were based on immature males of some unidentifiable conotylid (Shear 1974) and remain *nomina inquirienda*; no genuine trichopetalids have been found in the Great Plains or westward (a *Trichopetalum* specimen from British Columbia referred to by Shear [1971] seems likely to have been mislabelled or fortuitously imported; nothing like it has been collected since).

Trichopetalids have appeared in a number of more recent faunal lists (Shelley, 1978; Filka and Shelley, 1980; Holsinger and Culver, 1988; Reeves, 2000), a few new species of *Mexiterpes* have been added (Shear, 1982, 1986), and Lewis (2000) named a new *Scoterpes* from Indiana.

That brings us to the present day. The systematics and distribution of the Trichopetalidae prior to this study can be summarized in the following list, largely based on the recent checklist of North and Middle American millipeds by Hoffman (1999):

Family Trichopetalidae Verhoeff 1914
Mexiterpes Causey (1963): 7 species, all from Mexico
    Mexiterpes calenturas Shear (1982): caves in Tamaulipas

M. egeo (Causey) (1969): Cueva de el Puente, San Luis Potosi

M. fishi (Causey) (1969): caves in San Luis Potosi, Queretaro

M. metallicus Shear (1972): Pinal de Amoles, Queretaro

M. nogal Shear (1982): Sotano de Nogal, Queretaro

M. sabinus Causey (1963): Sotano del Arroyo, San Luis Potosi

M. sangregorio Shear (1986): Resumidero San Gregorio, Guerrero

Scoterpes Cope (1872): 5 species, all from USA

Scoterpes austrinus Loomis (1943): N. Georgia, Alabama

Scoterpes austrinus nudus Chamberlin (1946): Bartow Co., Georgia.

S. copei (Packard) (1881): Mammoth Cave system, Kentucky

S. dendropus Loomis (1939): Southcentral Missouri

S. ventus Shear (1972): Marion Co., Tennessee

S. sollmani Lewis (2000): Blue River Valley, Indiana

Trichopetalum Harger (1872): 13 species, from USA and Canada

Trichopetalum appropinquo (Causey, 1969): Washington Co., Maryland

T. cornutum Cook & Collins (1895): Michigan and Indiana, SW to North Carolina.

T. dux (Chamberlin, 1940): Durham Co., North Carolina

T. krekeleri (Causey, 1960): Randolph, Tucker Cos., West Virginia (caves)

T. lunatum Harger (1872): NE North America

T. montis Chamberlin (1951): Sevier Co., Tennessee

T. packardi (Causey, 1960): Virginia, West Virginia (caves)

T. quadratum (Loomis,1966: Prince Georges Co., Maryland

T. stannardi (Causey,1951): Clark Co., Illinois

T. subterraneum Causey (1967): Scott Co., Kentucky (cave)

T. syntheticum Shear (1972): Jackson Co., Alabama (cave)

T. uncum Cook & Collins (1895): Indiana and Kentucky, west to Missouri and Arkansas

T. weyerensis (Causey) 1960: Virginia, West Virginia (caves)

T. whitei (Ryder) 1881: Virginia, West Virginia (caves)

Trigenotyla Causey 1951: 2 species from USA

Trigenotyla parca Causey 1951: Carroll, Washington Cos., Arkansas

T. vaga Causey 1959: Latimer Co., Oklahoma

In addition to the new species described herein and in planned subsequent parts, several changes in the classification have resulted from detailed study. Perhaps the most significant is the recognition that *Scoterpes dendropus* Loomis (and two new, closely related species from Arkansas) is not a member of *Scoterpes,* differing from that genus in many respects. The new genus *Causeyella* is described below, with *dendropus* as its type.

In 1971, I described *T. syntheticum,* from Alabama, and argued that as a troglobite with *Trichopetalum*-like gonopods, it linked *Trichopetalum* and *Zygonopus.* That was

wrong, and *syntheticum* will be transferred later to *Scoterpes,* where it stands in a some-what isolated phylogenetic position as a highly derived species. The synonymy of *Zygonopus* with *Trichopetalum* is confirmed, however, by the discovery of a new epigean species in southern West Virginia that fits neatly between the two nominal genera in gono-pod anatomy. But because *Zygonopus* species clearly represent a monophyletic lineage within *Trichopetalum,* the name will be given the status of a subgenus. *Flagellopetalum* remains in the synonymy of *Trichopetalum*, but both *T. quadratum* and *T. appropinquo* appear to be synonyms of *T. stannardi* (all three originally described as species of *Flagel-lopetalum).*

Finally, a series of new species of very small trichopetalids, one species with ocelli and two eyeless (but not definitively known to be troglobites), form a coherent new genus, *Nannopetalum.*

My revision of this family will be published in two parts, to avoid the long delay that would be necessitated by the lengthy work still required on the larger, complex genera *Scoterpes* and *Trichopetalum.*

Gonopod Anatomy and Taxonomic Characters

Trichopetalids all look very much alike, even to the trained eye. It is usually possible to separate *Scoterpes* species from those of the other genera (even other troglobites) with-out seeing males because of the extremely long segmental setae, antennae and legs, but otherwise, lacking males, species determinations are very difficult. The small size of most of the species complicates matters. A few recent studies have shown that the female geni-talic structures, located behind the second pair of legs and called cyphopods, are of use in identifying species in many families of millipeds (chordeumatidans in particular), and it is probable that the same is true of trichopetalids. In fact, Scanning Electron Microscope observation of at least one species shows that the cyphopods are well-scelotized and com-plex. But even under high magnification of a compound microscope, the same details resolvable with SEM cannot be seen. If it were practical to use the Scanning Electron Microscope for routine determinations, it might be a different story, but the cyphopods are too small and too difficult to observe with readily available equipment to be of any use in making determinations. Therefore the female genitalia are not illustrated or described for any of the species below. But the situation is not entirely hopeless; since the geographic ranges of most of the species are now well-known, tentative assignments of names can be made on that basis, especially for the troglobitic species limited to caves in one or a few immediately adjacent counties.

The identification of species and their arrangement in a taxonomic and phylogenetic scheme therefore depends almost entirely on characters of the males. Unlike members of many chordeumatidan families, trichopetalid males are lacking in elaborate secondary sex-ual modifications, perhaps in keeping with their rather primitive status in the order. The legs anterior to the gonopods are more robust and longer than the legs posterior to the

gonopods, and one or more of the podomeres may be slightly modified to enhance the ability of the males to clasp the females during mating; this is most frequently seen on the sixth legpair (Figs. 15, 16). In the troglobitic species, such adaptations tend to be suppressed. There is not much of use, therefore, in these characters. The tenth and eleventh legpairs bear coxal glands, and the tenth coxa sometimes has a small, triangular coxal process, but again, the elaborate modifications seen in many chordeumatidans are not there.

That brings us down to the gonopods, on which we must rest almost the entire weight of any taxonomic and phylogenetic scheme. Fortunately, though trichopetalid gonopods are relatively simple, they are rich in characters that can be used not only to postulate species identity but to group species with their relatives.

The gonopods of the trichopetalids are the functional spermatophore-transfer devices, modifed from the eighth legpair. Each gonopod consists entirely of modified elements of the body of the coxa and of the extruded and sclerotized coxal gland. Some explanation is in order: in previous works I have referred to telopodites of the anterior gonopods of several chordeumatidan families, but I now believe that was a mistake. Telopodites are almost never present in chordeumatidan anterior gonopods, and when they are, they appear as small, often setose, rodlike structures with a clear articulation to the coxa. I am sure that what I had been calling telopodites in trichopetalids are in fact colpocoxites (the extruded and sclerotized coxal glands). The modifications of the rim of the coxal gland opening are called angiocoxites.

The sternum of the anterior gonopods is quite distinctive and characteristic of the family. In *Mexiterpes,* probably the most primitive genus (Shear, 1972), the sternum entirely surrounds the coxal elements of the gonopods and is well-sclerotized posteriorly. In all other genera, however, the posterior part of the sternum is much weaker and consists only of a poorly sclerotized, narrow band behind the angiocoxites. Anteriorly the sternum is characterized by two large swellings, one on either side, connected by a strong cuticular bar (i.e., Fig. 8). The lateral parts of the sternum above the swellings extends ventrally and forms definite sockets into which the bodies of the coxae are inserted and by which they are partially surrounded laterally. This form of the sternum does not occur in *Mexiterpes.*

The body of the coxa is oblong to subglobular and anteriorly setose. In *Mexiterpes,* the setae are numerous and not divided into groups, while the coxae extend posteriorly on each side, and these extensions may also bear a few setae. The division of the setae on the anterior face into two groups, usually a mesal group consisting of three setae, and a lateral group of five or more (Figs. 2, 9, 12, 13), seems to characterize all trichopetalids save *Mexiterpes,* but in *Causeyella,* the division into groups is obscure and the lateral setae are very numerous (Figs. 22, 23, 25). The lateral distal angles of the coxae may be drawn out into low projections, and most of the lateral setae occupy them. *Trigenotyla* species have coxal setae that tend to be ensiform, or sword-like, with broadened, flattened blades (Fig. 10). In *Trichopetalum* and *Nannopetalum,* setae are also found near the distal ends of the coxites, probably representing a dispersal of the lateral setal group (Fig. 2).

All *Trichopetalum, Causeyella,* and *Nannopetalum* have the anterior faces of the coxae more or less covered by tiny, acute, unsocketed trichomes, which become larger, longer, and almost hair-like distolaterally (Figs. 2, 8, 22, 23, 25). These are completely absent in *Scoterpes, Mexiterpes* and *Trigenotyla* (Figs. 12, 13, 17, 20).

The angiocoxites of the gonopods are projections of various forms from the distal parts of the coxae. Fundamentally there appear to be a pair of these on each gonopod, described previously by Causey as mesal and ectal. However, it is not entirely straightforward to homologize these coxites from species to species, since one of the pair may be lost, and the remaining coxite may develop a branch. The difference appears to be in detecting if a suspected coxite arises from the coxa itself, or from a bit of the way up another coxite. In both *Mexiterpes* and *Causeyella,* the ectal coxites lie directly posterior of the mesal coxites and are significantly smaller (Figs. 22, 23, 25). *Trigenotyla* species show intermediacy: one species has the *Causeyella* arrangement, two others have the ectal coxites in a fully lateral position, and a third seems to have lost them entirely. *Scoterpes* species ring nearly every possible change on the relative sizes and shapes of the coxites, but when both are present, the ectal coxite is always lateral and perhaps a little posterior to the mesal. In *Trichopetalum* and *Nannopetalum* it would appear that the ectal coxite has been lost in some, if not all species, but the mesal may be branched, sometimes quite complexly (Figs. 5, 8). The mesal coxite in these genera tends to wrap around the colpocoxite laterally.

The colpocoxites of *Mexiterpes* are medially fused and very much reduced; this would appear to be a synapomorphy for the genus. In the other genera, the colpocoxites are simple, large and subglobular (Fig. 3). A lobe may extend some distance posteriorly, and rest on a depression in the coxa of the ninth legs. In these genera, the colpocoxites are poorly sclerotized and often collapse or shrink on preservation or in the course of preparation for SEM viewing (Fig. 27). Arising from the colpocoxite, a distinct branch appears in almost all species that is more or less fimbriate, with extreme development seen in some of the species of *Causeyella* (Fig. 22). In *Trichopetalum* and *Nannopetalum,* the fimbriate branch is reduced (Fig. 3, 8), while in *Causeyella* it may become flattened and lamellate in two of the three species (Figs. 23, 25).

The ninth legpair have been traditionally referred to as the "posterior gonopods," but this nomenclature is technically not correct, since there is no evidence of any role in sperm or spermatophore transfer for these appendages. Therefore, in this work they will be referred to as ninth legs, and not as posterior gonopods. It would appear that their reduced form is simply an expedient to keep them out of the way while the anterior gonopods carry on mating. The sternum is small and weak, but often with obvious tracheal spiracles. The coxae are of nearly normal size and often have a dense tuft of setae apically, but never carry any kind of coxite (Figs. 4, 18, 24). In many species, vestigial coxal glands may be detected, or the coxae may be excavated on their anterior faces to accommodate the colpocoxites of the anterior gonopods. There may be an extension of the coxa beyond the artic-

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ulation with the telopodite; this is seen very distinctly in *Trigenotyla* (Fig. 21)*,* less so in *Causeyella* (Fig. 24)*.* The telopodite usually appears to consist of just one segment, but this obviously results from the reduction and fusion of all the segments distal to the coxae, as can be seen by the presence of a claw, rudimentary joints, and vestigial musculature. Further support for the homology of this podomere to the entire telopodite is provided by the occasional male in which the reduction has partially failed during development. In general, the ninth legs have little taxonomic value at the level of species, and are not illustrated here for all species.

Thus to summarize the gonopod anatomy of the trichopetalids, we see here perhaps the most primitive of anterior gonopods with regard to the colpocoxite retaining the lobe-like form of the extruded gland to which it is thought to be homologous. On the other hand, the telopodites have been completely lost. As in the other cleidogonoids, the ninth legs are simply reduced in size and podomere number, and very likely play no role in spermatophore transfer.

Behind the ninth legs, the tenth and eleventh legpairs carry coxal glands that evidently function in producing spermatophores, though exactly how this happens is very unclear. The one case in which spermatophores were found on both males and females of *Trichopetalum dux* (Chamberlin) is more mystifying than enlightening, since the spermatophores are complex and very large compared to the glands. One thought is that the glands provide only a secretion which hardens the spermatophores, which are molded into final form by pressing against the anterior gonopods. Aside from small triangular projections in a few *Trichopetalum* species, the tenth and eleventh coxae are unmodified (Fig. 19).

Taxonomy

At beginning of this section it seems appropriate to comment on the vexed subject of subspecies. Accepted taxonomic practice allows the description and naming of subspecies for distinctive populations within a species. Unlike full species, subspecies are not supposed to be reproductively isolated from other such populations. Therefore, in order to show that a population qualifies for subspecies status, authors should be able to point to specimens that are intermediate between the population in question and other, similar populations. Geographic factors should also be taken into account; a subspecific population should be geographically coherent and not scattered randomly across the species' range, nor should the subspecies be separated from the main range by a great distance or an unsurmountable barrier. In the former case the "subspecies" is more likely a simple genetic variant, and in the latter, a full species.

Unfortunately, many taxonomists fail to grasp the biological significance of the subspecies category, and seem to want to designate subspecies for populations which differ from theoretically conspecific other populations to a lesser degree than they think full species should differ--a typological approach. An example of this from the older literature on

trichopetalids was Chamberlin's 1946 description of *Scoterpes austrinus nudus*. As well, the labelling of Causey's collection of *Scoterpes* specimens shows many examples in which she changed the designation of populations from species to subspecies, and back again.

In this study, which involves many populations isolated in caves, considerable variation within species was noted, but because it either seemed chaotic or because the variant populations were linked with other populations of the same species along a continuum, this variation is not recognized by the naming of subspecies, but where appropriate, is discussed as fully as possible. In other cases, geographically isolated populations that differ slightly but consistantly from related congeneric ones are named as new full species, when if one applied the "degree of difference" criterion, they might have been called subspecies. For example, despite close similarity to *Trigenotyla vaga,* the new species *T. seminole* is consistantly distinct morphologically, no intermediates were found, and the two species are separated by the barrier of the Canadian River. The key is distinctiveness, not mere difference. Unbridged morphological gaps urge the hypothesis of separate species, regardless of how small or large the gap is.

My preference is thus not to name subspecies, but to recognize distinct populations as species, and to retain single names for species populations that vary, while describing the variation. The naming of a species is the presentation of a hypothesis that the population is reproductively isolated from other such populations. If it can later be shown that such is not the case, the hypothesis can be rejected and the name in question synonymized. While most species are still described on the basis of inference from morphological data, molecular studies may provide evidence of populations that are distinct only in their genetic makeup ("cryptic" species), or give us reason to synonymize species we once thought distinct. Such work has yet to be done for any milliped taxon.

Order Chordeumatida

Suborder Craspedosomatida

Superfamily Cleidogonoidea Shear, 1972

Family Trichopetalidae Verhoeff, 1914

Trichopetalinae Verhoeff, 1914:347.
Trichopetalidae Verhoeff, 1932:485. Hoffman, 1961:262; 1999:233 (list). Shear, 1972:274.

Type genus: *Trichopetalum* Harger 1872.
Included genera: *Trichopetalum* Harger 1872, *Scoterpes* Cope 1872, *Trigenotyla* Causey 1951, *Mexiterpes* Causey 1963, *Causeyella* n. gen., *Nannopetalum* n. gen.
Diagnosis: A family of Cleidogonoidea distinct in the modification of the ninth legs of males--reduction of the telopodite to a single fused article; great development of the seg-

mental setae; and in the (usual) presence of a strong fimbriate branch on the anterior gonopod.

Distribution: North America, from Newfoundland west to Wisconsin and south to Georgia, Alabama, Mississippi, Arkansas and Oklahoma (not present on the coastal plain from Virginia to Georgia or the Gulf Coastal Plain), highlands of northeastern and central Mexico.

Discussion: Causey (1959) established a tribe Scoterpini (*recte:* Scoterpetini) to include the genera *Scoterpes* and *Trigenotyla;* this was missed by Hoffman in his monumental *Checklist of the Millipeds of North and Middle America* (1999), although Causey's paper appears in his bibliography. Otherwise no division of the family into subordinate family-level taxa has been made. Causey considered trichopetalids to be a subfamily of Conotylidae (see Introduction, above); had she recognized the family Trichopetalidae as raised to that status by Verhoeff in 1932, she undoubtedly would have considered her tribe to be a subfamily. However, before deciding the validity of any subfamilial or tribal grouping of the trichopetalids, I would prefer to complete my work on the large genera *Trichopetalum* and *Scoterpes,* to be published in a subsequent part.

Genus *Nannopetalum,* new

Type species: *Nannopetalum pattersonorum,* n. sp.

Included species: In addition to the type, *N. vespertilio,* n. sp., and *N. fontis,* n. sp.

Diagnosis: Like *Trichopetalum,* members of this genus have 28 segments in both sexes, but differ in the structure of the gonopods; the mesal branch of the angiocoxite shows complex branching. Species of *Causeyella, Scoterpes* and *Trigenotyla* all have 30 trunk segments.

Distribution: Known from localities in the Appalachian Piedmont in Virginia, North Carolina and Alabama.

Discussion: These small millipeds are easily overlooked by collectors; I would expect at least several more species to turn up as the Piedmont region is sampled more thoroughly by various extraction methods. While *N. pattersonorum* is found in forest litter of at least two distinct habitats and has eyes, the other two species, depigmented and eyeless, have been collected from caves.

Nannopetalum as now comprised may not be monophyletic; each species has its peculiarities and may be assigned later to as yet undiagnosed genera when we know more about the tiny chordeumatids of the region.

The fimbriae referred to in the descriptions below are exaggerations of the trichomes found on the anterior faces of the gonopods of other trichopetalids.

Key to species

1a. With eyes, more than 5 mm long; Virginia. ....*pattersonorum*
1b. Eyeless, less than 5 mm long 2
2a. Segmental shoulders paranota-like; gonopods with prominent coxal fimbriae; North
 Carolina .... *vespertilio*
2b. Segmental shoulders moderately developed, not paranota-like; gonopods without
 obvious coxal fimbriae; Alabama ....*fontis*

Nannopetalum pattersonorum, **n. sp.**
Figs. 1–4

Types: Male holotype, 2 male paratypes and 3 female paratypes (FMNH) from Virginia,
Prince Edward County, Hampden-Sydney College campus, Wilson Trail, near stream in
maple-sycamore litter, collected 7 December 1988 by W. A. Shear. Male paratype
(FMNH) from same locality, but behind Gilmer Hall, in pine bark-fern litter, collected 15
November 1987 by W. A. Shear.

 Diagnosis: a larger species of *Nannopetalum* with seven (rarely six) ocelli on each
side of the head.

 Etymology: Named for Mr. and Mrs. Charles Patterson, whose generous bequest to
Hampden-Sydney College aided this work.

 Male holotype: Total length, 6.2 mm; width, 0.6 mm. Seven ocelli in T-shaped rows.
Unpigmented. Segmental setae 50% body width. Segments with pronounced lateral stria-
tions; segmental shoulders moderately developed. Legpairs 3–7 enlarged, pairs 3 and 4
the most robust, pairs 5 to 7 more slender but still markedly larger than postgonopodal
legs.

 Gonopods (Figs. 1–3) small, partly concealed. Sternal lobes moderately developed (*s,*
Fig. 1). Coxae (*cc,* Fig. 1) with 2 lateral setae each on moderate shoulders; angiocoxites
(*acx*, Fig. 1) strongly projecting basally, basal half set with typical trichomes, becoming
longer distolaterally; 3 basal setae; anterior process with 5–6 coarse teeth, 4 apical setae;
posterior process mesal, subtriangular, posteriorly curved. Fimbriate branch reduced.
Colpocoxites (*cc,* Fig. 1; Fig. 3) lobelike, squarish, small plumose processes on anterior
faces. Ninth legs (Fig. 4) as usual for the family; coxae slightly excavated on mesal side.
Legpairs 10 and 11 with coxal glands, otherwise unmodified.

 Female paratype: Total length 8.0 mm (extended specimens); width, 0.7 mm. Ocelli
7, curved row of 6, plus one out-of-row ocellus.

 Distribution: Definitely known only from the Hampden-Sydney College campus, but
six females taken in Prince Edward Co., Virginia, along the Bush River 3.2 miles north-
west of Meherrin, from beech litter, conform to this species. These specimens were col-
lected by me on May 15, 1977.
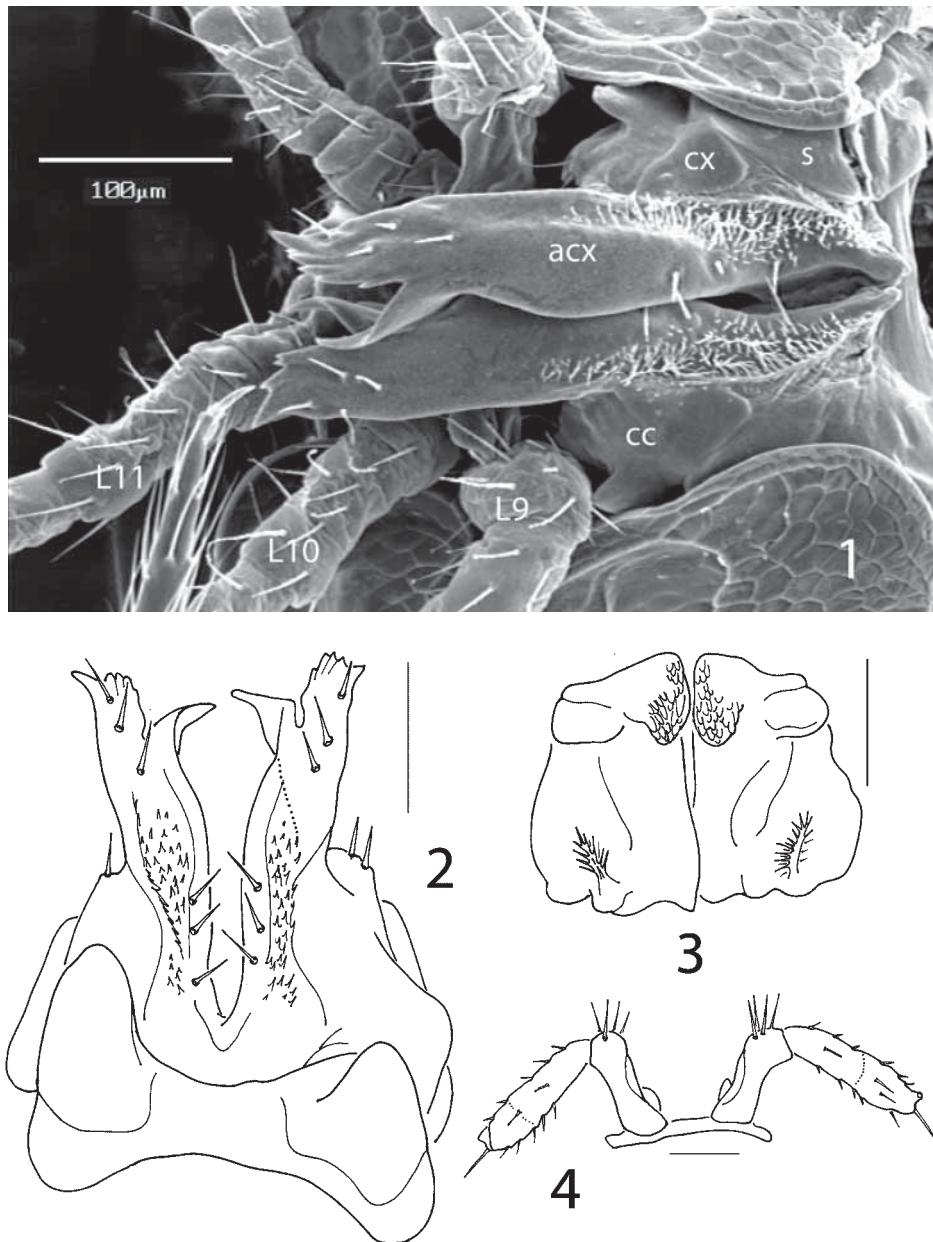
FIGURES 1–4. *Nannopetalum pattersonorum,* n. sp. 1, gonopod complex, ventral view (SEM). 2, gonopods, anterior view. 3, gonopod colopocoxites, anterior view. 4, male ninth legpair, posterior view. Scale lines = 0.1 mm (100 µm).

Discussion: Despite repeated sampling over the years of the exact spot where the types were collected, no further material came to light; however, none of these later samples were taken in winter. Finally, in January, 2003, a sample from the type locality contained a single male and two females.

Nannopetalum vespertilio, **n. sp.**
Figs. 5–7

Types: Male holotype from North Carolina: Henderson Co., Bat Cave, collected in the cave 14 May 1977 by C. Holler (NCMNS).

Diagnosis: A very small species of *Nannopetalum,* lacking ocelli; the gonopod fimbriae are large and prominent.

Etymology: The species epithet is a noun in apposition, "bat", and refers to the type locality.

Male holotype: Total length, 3.8 mm; width 0.4 mm. Ocelli absent. Unpigmented. Segmental setae 80% or more of body width, thin and curved; lacking prominent segmental striations; segmental shoulders well-developed, paranota-like. Legpairs three to seven encrassate, pair six the largest.

Gonopods (Fig. 5) with sternal lobes much reduced, shifted laterally; coxae with fimbriations becoming larger distally, eventually forming long, branched process; mesal setal group of three on each side shifted laterally; angiocoxites slender, median process short, acute, lateral process blunt, with two thin apical branches (Fig. 6); colpocoxites much reduced but with large fimbirate branches that appear to be basally fused. Ninth legs (Fig. 7) typical; tenth and eleventh legpairs with coxal glands, otherwise unmodified.
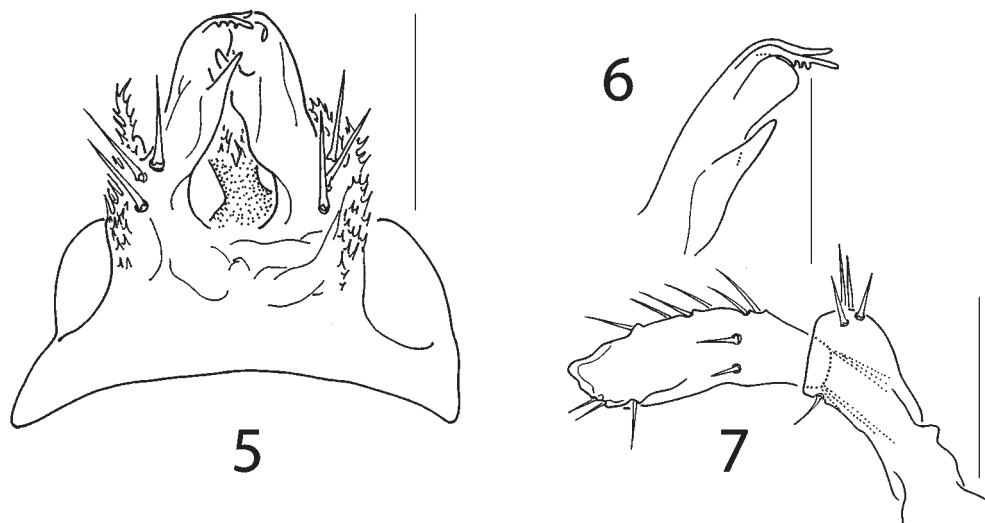
FIGURES 5–7. *Nannopetalum vespertilio,* n. sp. 5, gonopods, anterior view. 6, angiocoxite, mesal view. 7. male left ninth leg telopodite, anterior view. Scale lines = 0.1 mm (100 μm).

Female unknown.

Distribution: Known only from Bat Cave, an unusual granite fissure cave not located in a karst area.

Notes: It is not at all clear if this species is really troglobitic. It is the smallest known trichopetalid and one of the smallest of all chilognath millipeds.

Nannopetalum fontis, **n. sp**.
Fig. 8

Type: Male holotype and female paratype from Alabama: St. Clair Co., Springville Cave, Springville, collected 31 May 1962 by person or persons unknown ("DZ") (FSCA).

Diagnosis: Small, eyeless species with complex gonopods, especially the posterior branch; the gonopods have strongly reduced fimbriae.

Etymology: The species epithet is a noun, Latin for "of the spring or fountain," and refers to the type locality.

Male holotype: Total length, 4.75 mm; width 0.5 mm. Unpigmented; eyeless. Segments without evident lateral striations; segmental shoulders moderately developed. Legpairs 3–6 only slightly enlarged, legpair 7 about equal to legpair 12.

Gonopods (Fig. 8) with reduced coxosternum. Coxae (*c*) with median group of 2 setae shifted to posterior position, lateral group of 3 setae on prominent shoulders; angiocoxite branch complex (*ac*), with 4 terminations; anterior fimbriae reduced to a few hardly visible scales. Colpocoxites (*cc*) simple, large, lobe-like; fimbriate branch not seen. Ninth legs (*t9*) typical; prefemur with small terminal nubbin. Legpairs 10 and 11 with glands, coxae not modified.

FIGURE 8. Gonopods and ninth legs of *Nannopetalum fontis,* n. sp. Scale line = 0.1 mm (100 μm).

Female paratype: Total length, 4.5 mm; width, 0.5 mm. All somatic characters similar to male.

Distribution: Known only from the type collection.

Notes: The general appearance of members of this species is that of troglobites. In the vial with the type specimens were a female and an immature specimen of *Scoterpes*. There

are no other records of *Scoterpes* from Springville Cave, and the only species found in the vicinity is *S. syntheticum* (Shear). If the presence of a *Scoterpes* species in Springville Cave can be verified, this would be the first and only known case of syntopy between two troglobitic trichopetalids.

Genus *Trigenotyla* Causey

Trigenotyla Causey 1951:118; 1959:76. Shear, 1972:280. Hoffman, 1999:238 (list).

Type species: Trigenotyla parca Causey 1951.

Included species: The type, *T. vaga* Causey 1959, *T. blacki,* n. sp., and *T. seminole,* n. sp.
  Diagnosis: Closely related to *Causeylla,* but differing in the ninth legs of males, in which the coxae extend distal to the articulation with the telopodite. The anterior surfaces of the gonopod coxae lack trichomes. All species with 30 trunk segments; Causey (1951) originally stated that *T. parca* had 28 segments.
  Distribution: Northwestern Arkansas, northeastern and southcentral Oklahoma.
  Notes: Trigenotyla species are often, but not always, collected in caves; for many areas, caves are more heavily collected than forest litter habitats, and this may contribute to the preponderance of cave records for this genus. Only *T. blacki* seems restricted to caves, and only this species shows any troglomorphic adapatations (reduced eyes). It is also very likely that surface populations of Oklahoma *Trigenotyla* species are active and available for collection in the winter rather than the hot, dry summers that prevail in the region; little collecting is done in winter.
  The distribution of *Trigenotyla* as now understood can be divided into two distinct regions. *Trigenotyla parca* is known from caves and epigean sites in northwestern Arkansas, while *T. blacki* has been found in caves across the border in northeastern Oklahoma. The other region is in southcentral Oklahoma, in Seminole, Johnston, Murray, LeFlore, and Latimer Counties.
  Latimer County is the type locality of *vaga* and, with LeFlore County, is a good distance east of the other records. Causey labelled the more western collections as "profunda," suggesting that she believed them to be a new species. Unfortunately, the type of *T. vaga* is the only known male specimen, and the gonopods, originally mounted on a slide (AMNH), have been lost (L. Sorkin, pers. comm. 2002). I found that *Trigenotyla* south of the Canadian River in Murray and Johnston Counties closely conformed to the illustrations of *vaga* provided by Causey (1959), while there were differences in the specimens from Seminole County north of the Canadian. Therefore, I am naming the Seminole county specimens as a new species, *T. seminole,* and referring specimens south of the river to *T. vaga.*
  I predict that *Trigenotyla* species will be found generally in suitable habitats (caves, riverine forests) throughout eastern Oklahoma and western Arkansas when collectors are

in the right place at the right time. It also seems likely that the genus will turn up in south-western Missouri, southeastern Kansas, and northeastern Texas.

Trigenotyla gonopods are similar in general appearance to those of *Causeyella* species, but in some respects seem more apomorphic. The gonopod setae tend to be ensiform, distinctly so in *T. parca,* and are divided into two groups, with the typical 3 basal setae. The mesal coxite is broad in two species (*T. seminole* and *T. vaga*), thin and acute in *T. parca,* and absent in *T. blacki.* The ectal coxite in the former two species is very much like that of species of *Causeyella* and suggests that the latter two are apomorphic in the reduction of the structure. Trichomes are absent from the surfaces of the gonopod coxae, though under high magnification the coxae can be seen to be minutely roughened with tiny, conical projections. It is not clear at present if this is apomorphic (loss of trichomes) or plesiomorphic (partially developed trichomes).

The ninth legs of males are unique among trichopetalids in that the L-shaped coxa is extended distad to the articulation of the telopodite, a modification hinted at in some *Causeyella* species. Causey (1951) called the basal podomere a coxoprefemur, but if it is homologous to the same podomeres in other trichopetalids, it is the coxa alone, and the large distal joint includes the prefemur and other distal podomeres. In one species (*T. seminole*) there are tiny vestigial podomeres at the end of the prefemur. The form of the prefemur and the presence of these vestigial podomeres suggests that the telopodite article is only the prefemur, and unlike the situation in other genera, does not result from the fusion of other podomeres. The ninth coxa also has an unusually distinct, but likely vestigial, gland.

Key to species

Trigenotyla parca Causey
Figs. 9–12

Trigenotyla parca Causey 1951:118, figs. 1–5; Shear 1972:280. figs. 527, 528.
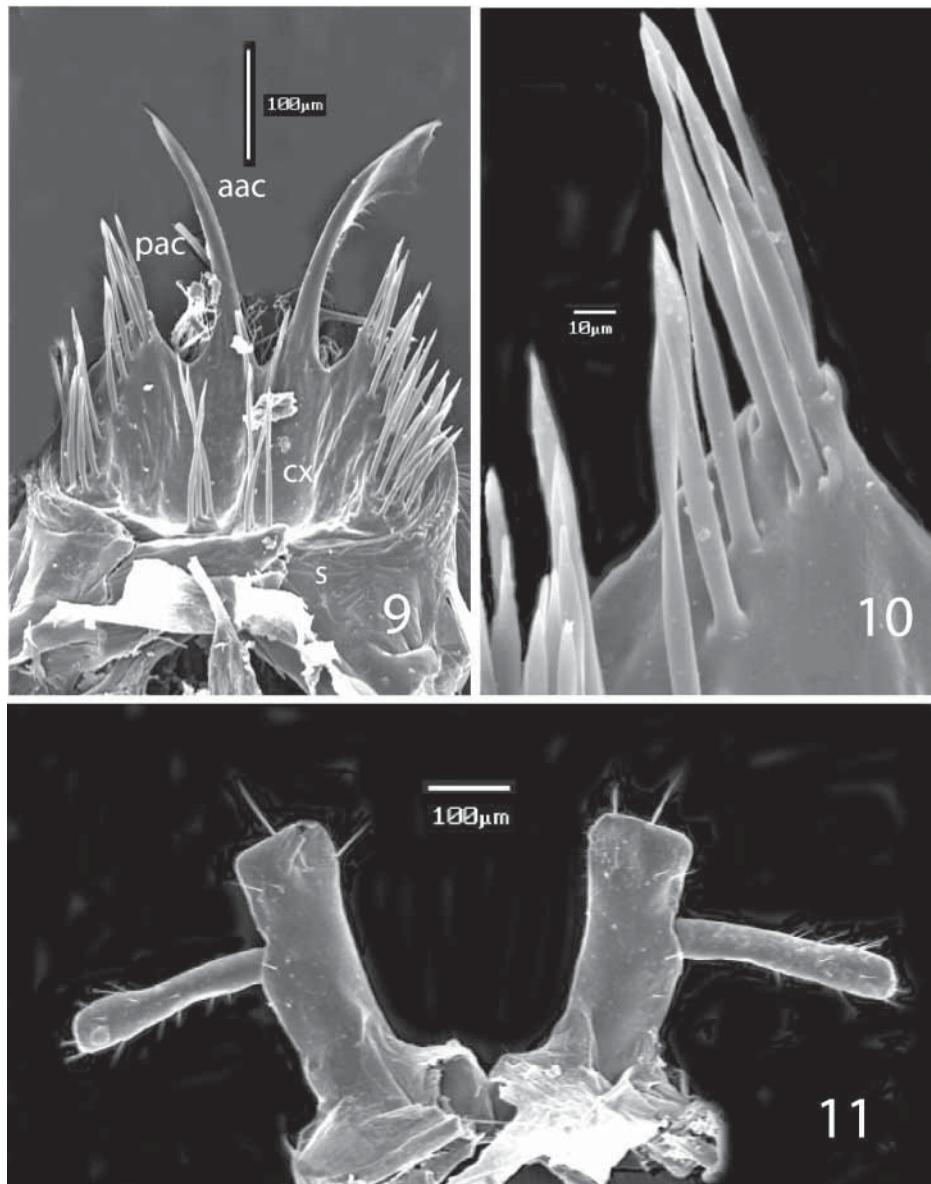
FIGURES 9–11. SEMs of *Trigenotyla parca* Causey. 9, gonopods, anterior view. 10, ensiform setae of gonopod, anterior view. 11, ninth legs of male, anterior view. Scale lines as labelled.

Types: Male holotype, 5 male and 5 female paratypes from Blue Spring, Carrol Co., Arkansas, collected 29 October 1949 (FSCA). Causey (1951) stated the types would be deposited in the collection of the Academy of Natural Sciences, Philadelphia, but there is no record they ever arrived there. Hoffman (1999) suggests, with a question mark, the Illinois Natural History Survey, where other specimens described in the same paper wound up, but the material is not to be found there, either. The Florida State Collection of Arthro-

pods received Causey's personal collection after her death. There I found specimens with the appropriate data labelled as paratypes, but unfortunately at some point the vial had been filled with water, not alcohol, and the specimens had rotted to bits. Another vial was labelled by Causey as "Trigentalum glesum Causey, male holotype, female paratype" and with the same collection data as given above. These specimens are undoubtedly the types of *Trigenotyla parca*. However, the gonopods of the male are missing, and while Causey's collection included a box of microscope slides on which trichopetalid genitalia had been permanently mounted, a slide of *T. parca* was not among them.
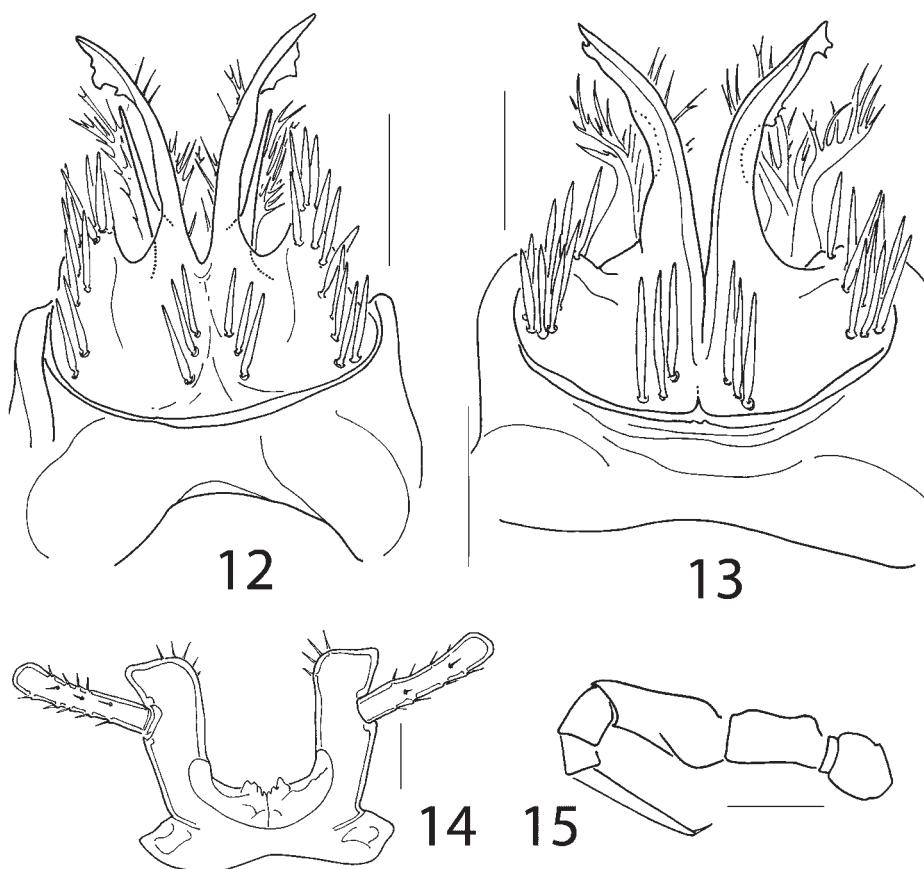
FIGURES 12–15. *Trigenotyla parca* Causey, 12, gonopods, anterior view. *Trigenotyla blacki* n. sp., 13–15. 13, gonopods, anterior view. 14, male ninth legs, anterior view. 15, male right sixth leg, posterior view. Scale lines for Figs. 12–14 = 0.1 mm (100 μm), for Fig. 15, 0.5 mm (500 μm).

Diagnosis: Distinct in the needle-like ectal coxite from *T. seminole* and *T. vaga,* where this structure is laminate and toothed; the latter two species also lack ensiform gonopod setae. In *T. blacki*, the ectal coxite is entirely missing.

Etymology: parca is a Latin adjective meaning (in this sense) "small." A more common meaning is "frugal, thrifty."

Male from Blue Spring: Length, 6.7 mm, width 1.0 mm. Color brown, mottled darker especially along dorsal midline. Segmental setae on midbody segments equal to segment width, segmental shoulders prominent, paranota-like. Fifteen to 17 ocelli in four irregular rows forming triangular eyepatch. Pregonopodal legs slightly crassate; femora of sixth legs enlarged, with distal ventral swelling.

Gonopods (Figs. 9, 12) with prominent sternal swellings; coxae (*cx*, Fig. 9) fused in midline, bearing two groups of prominent strongly ensiform setae (Fig. 10); lateral setal group of 16–22 arranged along lateral margins of coxae, distally raised on strong lobe at lateral distal margin. mesal group of 3 setae near midline. Anterior coxites (*aac*, Fig. 9) curved, acute, posterior edges irregularly serrate; ectal coxites (*pac,* Fig. 9) thin, needle-like; fimbriate branch relatively large (Fig. 12). Ninth legpair (Fig. 11) with L-shaped coxae bearing vestigial glands; telopodite of single article (prefemur) arises near midpoint on ectal side. Legpairs 10, 11 with coxal glands, otherwise unmodified.

Female from Blue Spring: 6.4 mm long, 0.9 mm wide, nonsexual characters as in male.

Distribution: Material examined: ARKANSAS: *Madison Co.:* Combs, no collector or date, male (FSCA). *Newton Co.:* Bat Cave, T15N, R23W, sec. 15, 8 June 1977, no collector, female (FSCA); Len House Cave, Buffalo National River, 15 July 1977, no collector, males, females (FSCA). *Washington Co.:* Granny Dean Cave, 10 mi S Fayetteville, 9 June 1969, S.& J. Peck, male (WAS); Devils Den State Park, 13 July 1949, M. W. Sanderson, L. Stannard, male (INHS).

Causey (1951) states that the species has been collected at "several places" in Washington Co., but I have seen no specimens aside from the records listed above. I predict that *T. parca* will be found generally throughout Arkansas north of the Canadian River, and probably also in adjoining Oklahoma and Missouri.

Notes: While it is likely that all the records are from caves, in two cases specific caves are not mentioned in the data. But trichopetalids are not likely to be captured outside caves in summer. The pigmentation and well-developed eyes suggest that *T. parca* is troglophilic, not troglobitic.

Trigenotyla blacki, **n. sp.**
Figs. 13–15

Types: Male holotype, one male and two female paratypes from Stansbury-January Cave, 4 mi. N of Colcord, *Delaware Co.*, Oklahoma, collected 13 January 1971 by J. H. Black (FSCA). The following specimens are paratypes: OKLAHOMA: *Delaware Co.:* Jail House Cave, 3 mi. N of Choleta, 1 January 1971, J. H. Black, juvenile; Bell's Bluff Cave, 5 mi. S of Jay, 14 July 1971, J. H. Black, male; Twin Cave, 5 mi. W, 3 mi. S of Jay, 29 November 1970, J. H. Black, female. *Adair Co.:* Cave #AD-14, 11 January 2003, G. Graening, D. Fenolio, male.

Diagnosis: The gonopod has ensiform setae like *T. parca,* but lacks an ectal coxite. *Trigenotyla blacki* has fewer ocelli, which are depigmented and in only two rows.

Etymology: for the collector, Jeffrey H. Black, recognizing his contributions (Black, 1971) to the biospeleology of Oklahoma.

Male holotype: Length, 6.5 mm, width 0.9 mm. Color pale yellowish, unmarked. Segmental shoulders moderate; segmental setae to 80% body width. Eight to eleven ocelli, not pigmented, irregular in size and well-separated, in two rows (typically of 6–7 and 3 ocelli). Pregonopodal legs somewhat more crassate than postgonopodal legs, legpairs 6 (Fig. 15), 7 largest; prefemora of 6 curved, with basal swelling.

Gonopods (Fig. 13) much as described for *T. parca,* but setae somewhat less ensiform, more clearly socketed, lateral group not raised on ectal shoulder; ectal coxites absent, mesal coxites more robust, fimbriate branch prominent. Legpair 9 (Fig. 14) as for *T. parca;* legpairs 10, 11 with glands, otherwise unmodified.

Female paratype: Length, 6.4 mm, width 0.85 mm. Nonsexual characters as in male.

Distribution: Known only from caves in Delaware and Adair Cos., Oklahoma.

Notes: Trigenotyla blacki, unlike the preceeding species, shows troglobitic adaptations in its reduced ocelli and pale pigmentation. As such it is presently the only troglobitic milliped known from Oklahoma.

Causey recognized this species as new, and labelled it "reducta," a name which was never published. Black (1971) lists "two undescribed species" of *Trigenotyla* from Oklahoma caves*,* as determined by Causey. However, the present study reveals that actually three species are involved (see below). The Delaware Co. records refer to *blacki,* those from Seminole Co. to *T. seminole,* new species, and those from Johnston and Murray Cos. to *T. vaga* Causey.

Trigneotyla seminole, new species
Figs. 16–19

Types: Male holotype, two male paratypes and one female paratype from Whiskey Cave, 9 mi. SE Bowlegs, Seminole Co., Oklahoma, collected 14 January 1974, by J. H. Black (FSCA). The following specimens (all collected in Seminole Co. by J. H. Black; FSCA) are paratypes: Doolin Cave, 8 mi NW of Sasakwa, 14 March 1974, male; Cold Springs Cave, 9 mi SE Bowlegs, 14 January 1974, female.

Diagnosis: Resembles *T. vaga* Causey in having gonopod ectal coxites broad in lateral view, differs in the shape of those coxites, smaller size and lack of pigmentation.

Etymology: The species name is a noun in apposition, for Seminole County.

Male holotype: Length, 5.0 mm, width 0.75 mm. Unpigmented. Segmental shoulders low; segmental setae (most rubbed off in type series) about equal to body width. Fourteen

to 17 round, well-pigmented ocelli in four rows forming triangular eyepatch. Pregonopodal legs enlarged, pair 6 (Fig. 16) the largest.

Gonopods (Fig. 17) with sternal lobes low; coxae not fused in midline; coxal setae not ensiform, in two groups, lateral group of 5 or 6 tightly clustered at distal ectal shoulder of coxa, mesal group of three near gonopod midline. Mesal coxites thin, evenly tapered, curved at tips, posterior edges not serrate; ectal coxites laterally flattened, in lateral view with 3 teeth. Ninth legpair (Fig. 18) typical of genus, but with 2–3 vestigial articles distal to prefemur; coxal glands prominent; legpairs 10, 11 (Fig. 19) with coxal glands, otherwise unmodified.

Female paratype: Length 5.0 mm, width, 0.8 mm. Nonsexual characters as in male.

Distribution: Known only from caves in Seminole Co., Oklahoma. All localites are north of the Canadian River, and it is hypothesized that this barrier separates the present species from the distribution of the closely related *T. vaga.*

Notes: Trigenotyla seminole populations are unpigmented or very lightly so, but have pigmented, well-formed, and numerous ocelli. Though the species has never been found on the surface, I suspect it is troglophilic, not troglobitic.

Causey had labelled all Oklahoma *Trigenotyla* (aside from the Delaware Co. collections described above as *T. blacki)* as "profunda," an unpublished name. This judgement is reflected in Black's (1971) treatment of Oklahoma *Trigenotyla.* However, Seminole Co. collections north of the Canadian River are clearly distinct from those south of the river in being smaller, less pigmented, and have differences in the gonopods and ninth legs. Thus they are named here as a new species.
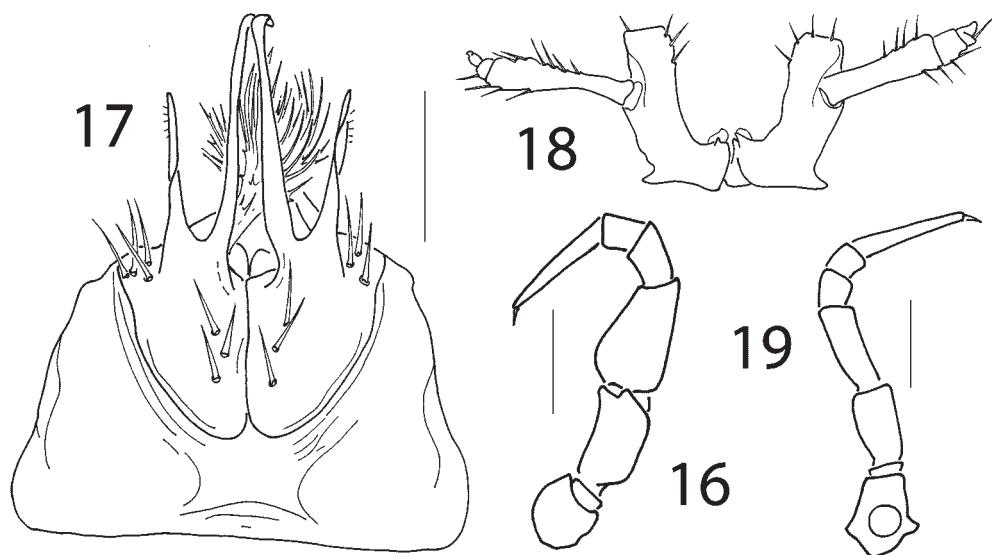
FIGURES 16–19. *Trigenotyla seminole,* n. sp. 16, male right sixth leg, posterior view. 17, gonopods, anterior view. 18, male ninth legs, posterior view. 19, male right eleventh legpair, anterior view. Scale lines for Figs. 17 and 18 = 0.1 mm (100 µm), for Figs. 16 and 19, 0,5 mm (500 µm).

Trigenotyla vaga **Causey**
Figs. 20, 21

Trigenotyla vaga Causey 1959:76, figs. 1, 2.

Types: Male holotype from "a river ravine," Latimer Co., Oklahoma, collected 9 December 1933 by J. R. Carpenter (AMNH). The body of the male holotype is in the American Museum collection, but the gonopods are not. According to a label in the type vial, the gonopods were mounted on a microscope slide; the slide cannot be found (L. Sorkin, pers. comm. 2002). A box of slides of trichopetalid gonopods is in the FSCA but one of *T. vaga* is not among them. Absent the crucial information from the gonopods, we must rely on Causey's original description and drawings to establish the identity of *T. vaga.* Fortunately the drawings are good ones and show a number of salient features; they were probably made from the slide using a camera lucida or similar device.

Etymology: The species name is a Latin adjective, "wandering," and doubtless refers to the distance separating it from *T. parca.*

Diagnosis: very similar to *T. seminole* but differing in the broader gonopod ectal coxites, larger size and definite pigmentation. Besides these features, Causey's drawings show the fimbriate branch as lamelliform, as seen in two new species of *Causeyella* described below. The branch is more typically fimbriate in the material I have seen from Murray and Johnston Cos. The specimens from Wild Woman Cave described below are much paler than surface-collected ones, but otherwise do not seem to show any adaptations for cave life. Specimens from in or near Latimer Co. are required to safely pin down the identity of the Murray and Johnston Cos. specimens.
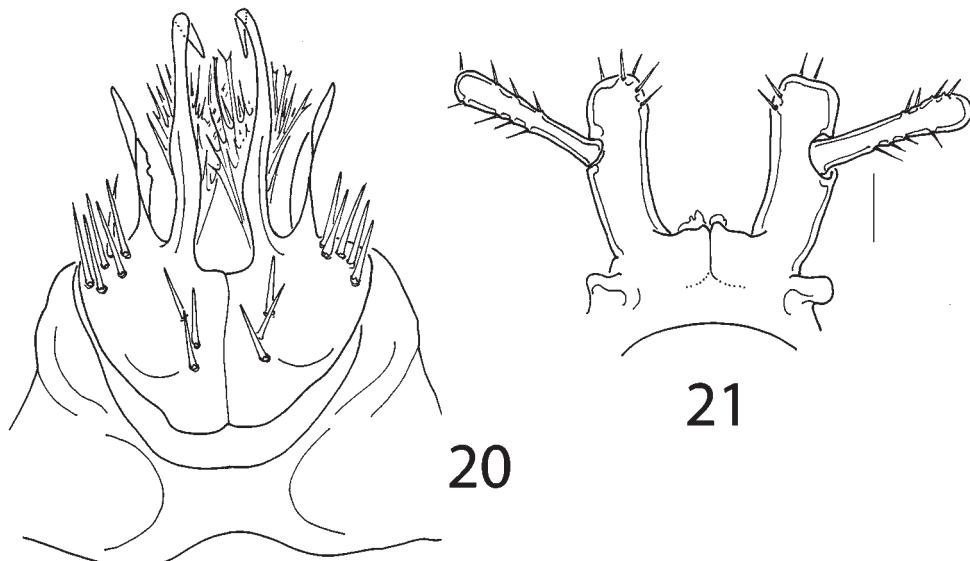
FIGURES 20, 21. *Trigenotyla vaga* Causey. 20, gonopods, anterior view. 21, male ninth legs, posterior view. Scale lines = 0.1 mm (100 μm).

Male from Wild Woman Cave: Length, 6.5 mm, width, 0.9 mm. Segmental shoulders pronounced, segmental setae nearly equal to body width. Color pale yellow to gray. Ocelli 15–17 in triangular eyepatch.

Gonopods (Fig. 20) much as in *T. seminole,* differing in greater breadth of ectal coxite, tighter clustering of lateral setal groups. Ninth legpair (Fig. 21) as in *T. parca,* lacking vestigial terminal joints. Tenth and eleventh legpairs with coxal glands.

Female from Wild Woman Cave: Length, 6.3 mm, width 0.9 mm. Nonsexual characters as in male.

Distribution: Material examined (all FSCA): OKLAHOMA: *Murray Co.:* Wild Woman Cave, R. Harrell, 7, 28 February 1959, 2 March 1962, R. Harrell, 3 males, 3 females; Bitter Enders Cave, 29 December 1973, J. H. Black, male, female. *Johnston Co:* Horse Thief Cave #2, 4 mi. SE of Pontotoc, 12 May 1970, J. H. Black, female. *LeFlore Co:* Choctaw Nation Historic Site, 27 September 2002, C. T. McAllister, female, probably this species. Literature Records: Black (1971) reported the Wild Woman Cave and Horse Thief Cave #2 records, but confounded under "*Trigenotyla* sp." probable records of *blacki, seminole* and *vaga.*

The type locality is inexactly located, so on Fig. 33 the Latimer County record is simply indicated as the approximate center of the county. The LeFlore County record is of interest because the site is literally only a few meters from the border of Oklahoma with Arkansas, and makes it almost certain that *T. vaga* will be found in the latter state. Likewise, because of the continuity of habitat, I would expect this species to eventually be recorded from Texas. All *T. vaga* records to date are from south of the Canadian River; this stream appears to be an effective barrier separating *vaga* from the other species.

Genus *Causeyella,* new

Scoterpes, Loomis 1939:181 (not *Scoterpes* Cope 1872)

Type species: Scoterpes dendropus Loomis 1939

Included species: Besides the type, *Causeyella causeyae,* n. sp., and *C. youngsteadtorum,* n. sp.

Diagnosis: Blind, unpigmented, and with thirty segments, as in *Scoterpes,* but differing from that genus in the gonopods, in which the ectal coxites are placed directly posterior to the mesal, and in having the front faces of the coxae with trichomes. The gonopods are similar to those of *Trigenotyla* species, but in *Causeyella* the coxae of the ninth legs are not strongly extended beyond the joint with the telopodite, and the anterior gonopod coxal faces lack ensiform setae. Prominent trichomes are present on the gonopod coxae of *Causeyella* species; these are absent in *Trigenotyla.* Species of *Causeyella* also average nearly twice the body length of species of *Scoterpes* or *Trigenotyla.*

Etymology: For the late Nell Bevel Causey, in recognition of her extensive work on trichopetalids.

Distribution: Caves in southwestern Missouri and northern Arkansas.

Notes: No new descriptive information on any *Causeyella* species has appeared since 1939. *Causeyella* species are all evident troglobites of long standing, eyeless and unpigmented and with long legs and antennae. They are the largest trichopetalids, running up to 12–13 mm long, about twice the length of typical *Scoterpes* species, and nearly three times as long as *Nannopetalum vespertilio,* the smallest known trichopetalid. After studying a full range of species of *Scoterpes,* one is struck by how divergent *dendropus* is from the other species originally placed in that genus. The two new Arkansas forms confirm the distinctiveness of this group of closely related species and at the same time point to a definite relationship with *Trigenotyla,* also from Arkansas (and Oklahoma). My remarks in 1972 (taken at face value by Peck and Peck, 1982) that *Scoterpes* and *Trigenotyla* might someday have to be combined was based on consideration of *S. dendropus* as a typical *Scoterpes,* which it turns out not to be.

Scoterpes dendropus was described by Loomis in 1939 from Marvel Cave, Stone Co., Missouri, and has been subsequently recorded from other caves in Stone, Barry and Taney Counties. The first mention of the genus for Arkansas was by McDaniel and Smith (1976), who quote Causey (in litt.) to the effect of the presence of two new species in the state. Youngsteadt and Youngsteadt (1978) combine these two species in their records as "*Scoterpes* sp. MS." Records of *Scoterpes* from southeastern Missouri (Jefferson and Franklin Counties, "unspecified sites" in Peck and Lewis, 1978) seem to be in error or may be based on misidentifications of *Austrotyla specus* (Loomis). In my 1972 monograph, I made reference to, and mapped, a record of *dendropus* for Illinois Caverns, Monroe County, Illinois. Peck and Lewis (1978) call this "an old M. W. Sanderson record" but make no further reference. Sanderson's collections are for the most part in NHSI, but no Illinois *Scoterpes* can be found there. In a recent survey of cave life in southwestern Illinois, Lewis et al. (2003) were not able to verify any Illinois records of *Causeyella.* Given the extensive work done on the cave faunas of Missouri and Illinois, I think it unlikely that *Causeyella* from Illinois or from southeastern Missouri would have been overlooked, and these records should be deleted.

As it now stands, the three species of *Causeyella* occupy three fairly disjunct areas, but all in the White River drainage. The species status of these populations is based on my ability to consistantly separate them, but it is possible that more detailed collecting work in northern Arkansas may reveal intermediates. More biogeographical notes are provided in the species accounts, but to summarize, *Causeyella dendropus,* except for one Arkansas record (Fig. 33) is found north of the White River, *youngsteadtorum* (again but for a single record) confined to the region between the White and Buffalo Rivers, and *causeyae,* the easternmost species, is found on both sides of the White River.
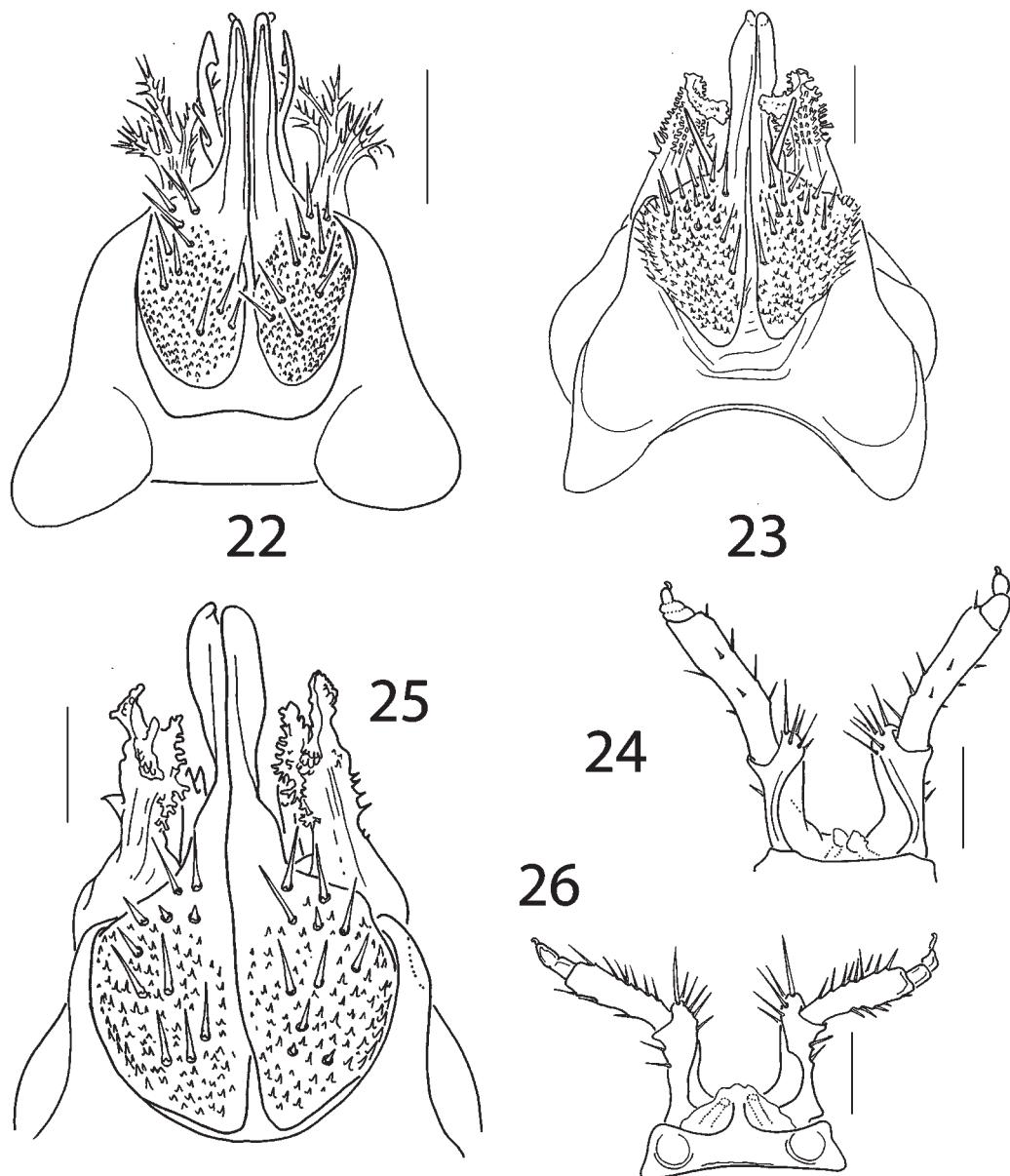
FIGURES 22–26. *Causeyella dendropus* Loomis, 22, gonopods, anterior view. *C. causeyae,* n. sp., 23, 24. 23, gonopods, anterior view. 24, male ninth legs, anterior view. *C. youngsteadtorum,* n. sp., 25, 26. 25, gonopods, anterior view. 26, male ninth legs, anterior view. Scale lines = 0.1 mm (100 μm) for Figs. 22, 23, 25, 0.5 mm (500 μm) for Figs. 24, 26.

Key to species

1a. Colpocoxite branches of gonopods fimbriate (Fig. 22); ectal coxite nearly as long as mesal; SW Missouri, NW Arkansas.. *dendropus* (Loomis).

1b. Colpocoxite branches of gonopods lamellate (Fig. 23, 25); ectal coxite no more than half as long as mesal; N Arkansas..2

2a. Frontal setae of coxites acute; fimbriae short; mesal coxite distinctly spatulate in anterior view (Fig. 25); Boone and ?Newton Cos., Arkansas ....*youngsteadtorum,* n. sp.

2b. Frontal setae of coxites blunt; fimbriae long; mesal coxite not as distinctly spatulate in anterior view (fig. 23); Independence, Stone and Izard Cos., Arkansas ....
....*causeyae,* n. sp.

Causeyella dendropus (Loomis)
Fig. 22

Scoterpes dendropus Loomis, 1939:181–182, fig. 9.

Types: Male holotype from Marvel Cave, Stone Co., Missouri, collected 27 June 1938 by Kenneth Dearolf (MCZ).

Diagnosis: Distinct from the two Arkansas species in having the colpocoxite branch finely fimbriate and the ectal coxite nearly as long as the mesal.

Male from Marvel Cave: Length, 12.5 mm, width, 1.1 mm. Unpigmented, eyeless. Segmental shoulders well developed, paranota-like; segmental setae slightly more than half pleurotergal width. Pregonopodal legs slightly enlarged, no podomeres modified. Gonopods (Fig. 22) with large, bulbous coxae bearing fine, scale-like trichomes on anterior surfaces; coxal setae normal, acute, about 10 on each coxa, 3 basalmost form group slightly separated from others. Mesal coxites rodlike, evenly tapering, not spatulate, longer than ectal coxites. Ectal coxites basally broad in lateral view, with long anterior branch and two short posterior branches appearing as acute teeth. Fimbriate branch large, not extending anteriorly. Colpocoxites lobular, rounded, poorly sclerotized. Ninth legs typical, coxae laterally flattened, with vestigial glands, prefemora fusiform, small distal articles with distinct articulation and spine-like claw. Coxae 10 and 11 with glands, not modified.

Female from Marvel Cave: Total length, 13 mm, width 1.4 mm. Nonsexual characters as in male.

Distribution: Specimens examined (all FSCA): MISSOURI: *Barry Co,*, Rockhouse Cave, 7 Sept. 1959, J. Tocklen, male. *Stone Co.*, Marvel Cave, 2 April 1959, T. C. Barr, 6 males, 4 females; Gentry Cave, 3 May 1958, no collector, male, female; Old Spanish Cave, 26 January 1958, T. C. Barr, female. *Taney Co.*: Tumbling Creek Cave, Ozark Underground Laboratory, 21 June 1969, T. Aley, D. Walley, female. ARKANSAS: *Newton Co.:* Fitton Cave, 14 December 1963, R. Martin, male; 13 May 2001, G. Greening *et al.,* male. Literature records: MISSOURI: *Barry Co.*: Buck Ridge Cave, Chimney Rock Cave, Sweet Potato Cave (Gardner, 1986), Radium Cave (Elliott, 2002). The whereabouts of the specimens on which these records were based is not known, but they are within the range

of *C. dendropus* and no other troglobitic trichopetalids occur in these counties. Sutton (1993) reported the species from Adams Cave #1, Oregon Co., but this is much closer to the range of *C. causeyi* than it is to that of *dendropus*. The specimen was immature and found in company with many more individuals of the widespread troglobitic tingupid milliped *Tingupa pallida* Loomis. McDaniel and Smith (1976) recorded *dendropus* from Newton and Carroll Cos., Arkansas. I have not seen any specimens from Carroll Co., and aside from the general statement from McDaniel and Smith (1976), no detailed collection data. I was inclined to dismiss the Arkansas records of *dendropus* as curatorial errors, but the discovery of a second male from Fitton Cave in 2001 seems to prove that *dendropus* indeed occurs in Arkansas, impinging on the range of the quite distinct *younsteadtorum*. This is also the only verified record from south of the White River, which theoretically could serve as a barrier between *dendropus* and *youngsteadtorum*. More collecting is needed in northwestern Arkansas (Benton, Carroll, Washington and Madison Counties) to delineate the ranges of the two species. Unfortunately 2001 collections of *Causeyella* from Joyce Cemetary Cave in Benton Co. were all females. The putative records of *dendropus* (as a *Scoterpes*) from southeastern Missouri and from Illinois have already been discussed in the generic account; they probably are in error.

Causeyella causeyae, **n. sp.**
Figs. 23, 24

Types: Male holotype, male paratype and 2 female paratypes from ARKANSAS, *Independence Co.*, Foushee Cave, 6 miles west of Locust Grove, collected by unknown person or persons, May, 1978 (FSCA). The following are paratypes: ARKANSAS: *Independence Co.*, Cushman Cave, 0.5 miles from Cushman, 8 July 1974, G. Harp, four males, 3 females; Dodd Cave, 14 December 2001, G. Greening, D. Fenolio, male (SBP). *Izard Co.*, Clay Cave, 7 mi SW Melbourne, 11 October 1974, G. Harp, numerous males and females; Donovan Cave, 2 mi SW Calico Rock, 24 January 1964, D. Martin, male; Goat (Prison) Cave, 22 November 2002, B. Wagner, D. Kempwerth, male (SBP). *Stone Co.*, Hell's Creek Cave, 2.5 mi N Mountain View, 26 January 1974, V. R. McDaniel, 2 males; Blanchard Springs Cave, 27 September 1967, T. C. Barr, juveniles probably this species; Rowland Cave, 12 June 2001, G. Greening et al., male (SBP); Alexander Cave, 24 March 2001, M. Slay, L. Moritz; Gustafson Cave, 6 October 2002, G. Graening et al., male (SBP).

Diagnosis: A large (13.5 mm long) species of *Causeyella* with lamellate branches of the gonopod colpocoxites; frontal coxal setae somewhat thickened and blunt.

Etymology: For Nell Bevel Causey.

Male holotype: Length, 13.5 mm, width 0.9 mm. Unpigmented, eyeless. Segmental shoulders well developed, paranota-like; segmental setae 65–70% of body width. Legpairs 3–7 noticeably enlarged compared to legpairs 12 and posterior; no podomeres modified. Gonopods (Fig. 23) with well developed sternal lobes. Anterior surfaces of coxae

entirely covered with prominent scaly trichomes becoming larger distally; about 15 setae on each coxa, not separated into groups; mesal coxites in anterior view slightly spatulate, ectal coxites only about half their length, broad in lateral view. Lamellate branch of colpo-coxite very large, curled at tip, roughened with rows of blunt trichomes, extending anterior of mesal coxites. Ninth legpair (Fig. 24) with coxae laterally flattened, mesally excavated, bearing vestigial glands, articulation of prefemora offset laterally; prefemora longer than coxae, two or three vaguely indicated articles distally, claw short, twisted. Legpairs 10, 11 with glands, unmodified.

Female paratype: Length, 13.5 mm, width 1.05 mm. Nonsexual characters as in male.

Distribution: Independence, Stone, and Izard counties, ARKANSAS, as listed under "Types" above. Literature records: ARKANSAS: *Izard Co.,* Bergren Cave, Needles Cave; *Stone Co.*, Hell Creek Cave (as "*Scoterpes* n. sp." in McDaniel and Smith, 1976). These records were not verified; the wherabouts of the specimens are unknown. It appears that this species occurs on both sides of the White River. Records of "*Scoterpes*" from Oregon Co., Missouri (see under *C. dendropus* above) may be *C. causeyae,* but are probably in error.

Causey labelled examples of this species as "Scoterpes martini*"* or "Scoterpes dendro-pus ssp. martini.*"*

Causeyella youngsteadtorum, **n. sp.**
Figs. 25–32

Types: All specimens, FSCA. Male holotype, female paratype from ARKANSAS, *Boone Co.*, Brewer Cave (T16N, R18W, S8), collected July/August 1976 by Norman and Jean Youngsteadt. The following specimens are paratypes: ARKANSAS: *Boone Co.,* Major's Cave (T16N, R20 W, S16), July 1977, N. and J. Youngsteadt, 3 females. *Newton Co.:* Lewis Spring Cave (T16N, R19W, S12), January 1976, N. and J. Youngsteadt, male, female; "Cave" (T17, R19W), June/July 1976, N. and J. Youngsteadt, male, female. *Searcy Co.:* Hurricane River Cave (T16N, R13W, S7), N. and J. Youngsteadt, January/ February 1976, male; Woods Hollow Cave #1, 16 March 2002, G. Greening, C. Brickey (SBP); Thruway Cave, 31 July 2002, M. Slay, male, female (SBP).

Diagnosis: Very similar to *C. causeyae,* but the ectal angiocoxites are more spatulate, and the mesals are shorter and have two subequal apical teeth.

Etymology: named for Norman and Jean Youngsteadt, in recognition of their collection of nearly all known specimens of this species and their contributions to Arkansas bio-speleology.

Male holotype: Nonsexual characters as described for *C. causeyae.*   Gonopods (figs. 25, 27–29) with well developed sternal lobes. Anterior surfaces of coxae entirely covered with prominent scaly trichomes not becoming notably larger distally; about 15 setae on each coxa, not separated into groups; mesal coxites (*aac,* Figs. 27, 29) in anterior view

strongly spatulate, ectal coxites (*pac*, Fig. 29) less than half their length, broad in lateral view, with subequal apical teeth. Lamellate branch of colpocoxite (*fb,* Figs. 27, 29) very large, curled at tip, posteriorly divided into 3–4 smaller branches, roughened with rows of blunt trichomes, extending anterior of mesal coxites. Ninth legpair (Figs. 26, 31) with coxae laterally flattened, mesally excavated, bearing vestigial glands, articulation of prefemora offset laterally; prefemora longer than coxae, two or three vaguely indicated articles distally, claw short, twisted. Legpairs 10, 11 with glands, unmodified.
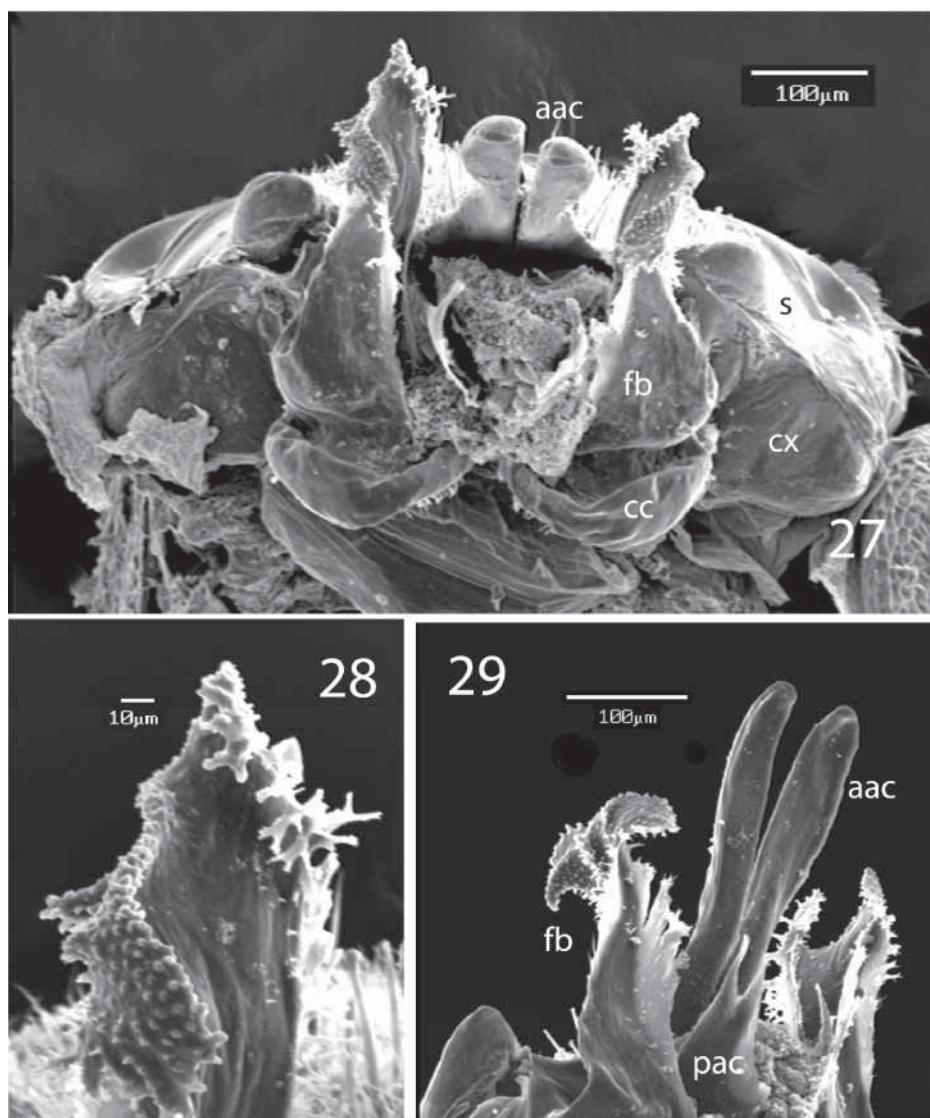
FIGURES 27–29. SEMs of *Causeyella youngsteadtorum.* 27, gonopods, ventral view. 28, gonopod fimbriate branch. 29, gonopod tips, oblique lateral view. Scale lines as labelled.
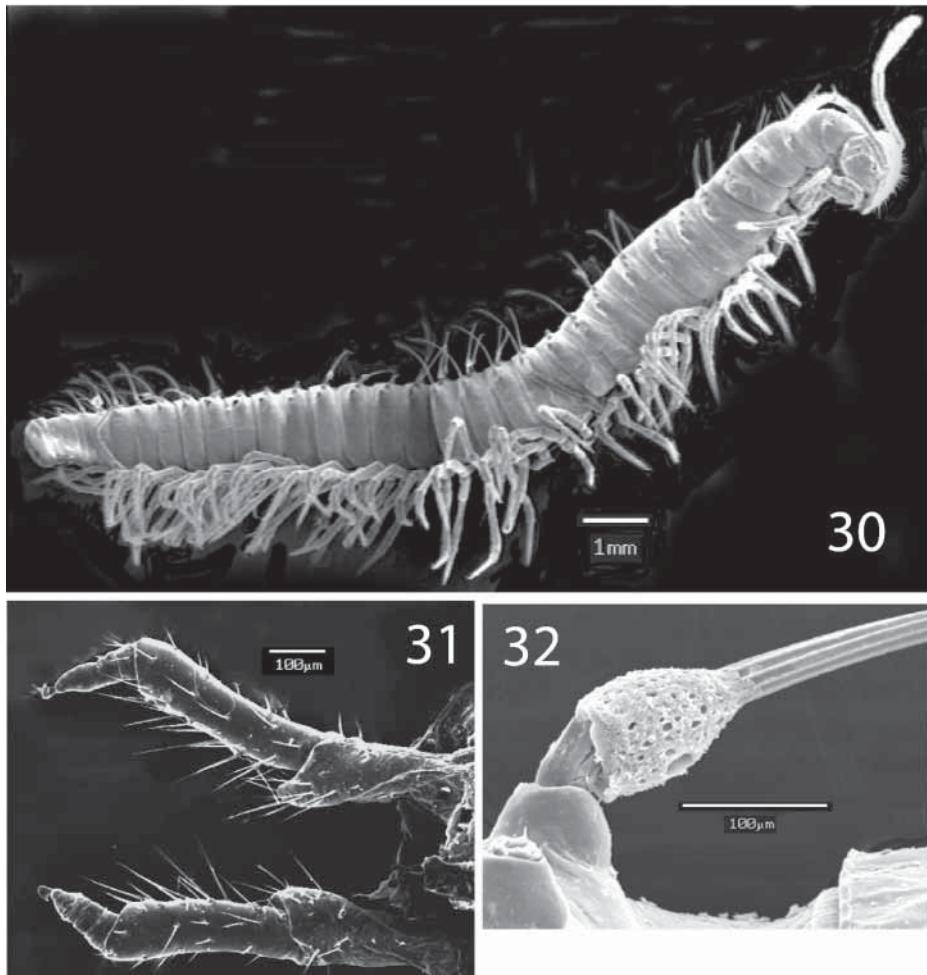
FIGURES 30–32. SEMs of *Causeyella youngsteadtorum.* 30, female, lateral view. 31, ninth legs of male, anterior view. 32, outermost segmental seta of left side of segment 12, showing typical secretion. Scale lines as labelled.

Female paratype: Length, 13.5 mm, width 1.05 mm. Nonsexual characters as in male. Intact female depicted in Fig. 30.

Distribution: As given under Types, above. Literature records: Youngsteadt and Youngsteadt (1978) record the species from Potato Cave, Searcy Co., very close to Hurricane River Cave, but these specimens were not found with the others from their survey in the Causey collection. Fitton Cave and Peccary Cave in Newton Co. were not visited by the Youngsteadts in their survey of northern Arkansas caves (Youngsteadt and Youngsteadt, 1978), but as detailed above under *C. dendropus,* at least the former cave supports that species. Except for one record (Fig. 33), *youngsteadtorum* occurs in the region south of the White River, but north of the Buffalo River. The Buffalo River flows in a deep gorge and may be enough of a barrier to separate *youngsteadtorum* from *causeyae.*
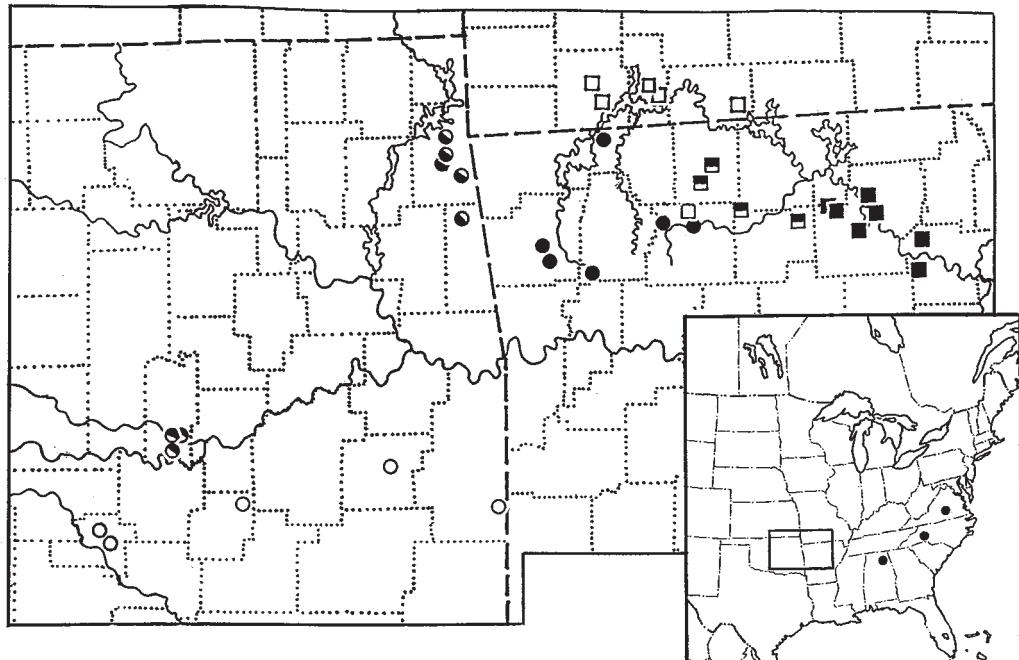
FIGURE 33: Inset map shows the eastern and midwestern United States; filled circles are records of species of *Nannopetalum,* box shows area of larger map (parts of Oklahoma, Arkansas and Missouri). On larger map, dashed lines are state borders, dotted lines county borders; open squares, *Causeyella dendropus;* filled squares, *C. causeyae;* half-filled squares, *C. youngsteadtorum;* filled circles, *Trigenotyla parca;* open circles, *T. vaga;* circles with lower half filled, *T. blacki;* circles with upper half filled, *T. seminole.*

The late Dr. Nell B. Causey, with the help of speleobiologists Drs. Barr and Peck, Dr. John Holsinger, and Dr. Harrison Steeves, amassed a very large collection of trichopetalids and had sorted them out into morphospecies, many of which were labelled with manuscript species or subspecies names. After her death, her collection was deposited in the Florida State Collection of Arthropods, located in Gainesville, Florida. I have not always agreed with Dr. Causey's taxonomic decisions in this study, but my task of determining species limits in this complex family was made considerably easier by her previous work. Because Dr. Causey had widely disseminated information about her manuscript species to speleobiologists, I have briefly discussed her use of names under each of the species she studied. This paper is respectfully dedicated to her memory. As usual, the aid of Asa Kreevich was invaluable.

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